a way that does not unnecessarily limit the amount of available target DNA.

Blood sampling, e.g. from the ulnar vein as described by ARCTANDER (1988), can be done even in small birds without harming the animal. Two points are important here:

(1) In small birds one should not try to insert a syringe into the blood vessel. Rather, one should puncture the vessel, wait for a drop of blood to form, and take up the blood into a glass capillary by capillary action. Alternatively, a few drops of blood can be soaked up on a piece of clean tissue which is then immersed in ethanol (or an appropriate buffer).

(2) Syringes and capillaries should not be heparinized and preservation buffer should not contain heparin. Clotting of blood, which occurs immediately in ethanol, is not a problem for later DNA extraction, so any anticoagulent is superfluous. Heparin will intercalate with the DNA double helix and thus block the PCR reaction. Although heparin can enzymatically be removed from blood samples if needed, this is expensive and should be avoided.

Taking blood form a bird can be done very quickly by a single person, although two people, one holding the bird, the other taking the blood, are preferable with large birds. Careful studies have shown that, if done properly, blood sampling does not have any negative effects even in small birds (ARDERN et al. 1994). In nestlings or moulting birds it is possible, of course, to obtain tissue by plucking a growing feather and preserving the basal part of the feather that contains highly vascularized living tissue. In that case the tissue-containing tip of the feather shaft should be cut off, split open and then be submerged in ethanol (or buffer).

4. ROLE OF MUSEUMS

Museum collections will be increasingly important in providing material not only for morphological, but also for molecular studies. As with specimens, they should function as repositories of material that is freely available to the scientific community. Obtaining adequate material for tissue collections is much easier than obtaining animals appropriate for specimen preparation. Animals collected or sampled in the wild, those that died in zoos or bird parks, victims of collisions with human-made structures (windows, wires) or even fresh road kills are a perfectly good sources of material for molecular analysis. Many species can be sampled at bird-ringing stations or on ringing expeditions. It is worth keeping in mind, though, that samples from birds of known breeding status with exact geographic origin are scientifically more valuable than samples from migrants caught during routine operations at fixed ringing stations.

Given the minimal technical requirements and cost involved, I strongly encourage all museums to build up tissue collections in addition to their specimen holdings. Whenever possible, the entire animal should be kept as a voucher specimen. However, there are many reasons why this may not be feasible: conservation or ethical considerations (especially in large and rare species), lack of permits to kill an animal, taxidermists' work hours involved in preparing a specimen, space requirements for storage, labour of collection maintenance etc. Also, in population-genetic and phylogeographic studies requiring large sample sizes it may not be feasible to preserve all specimens from which samples are taken. For instance, in a phylogeographic study of the *Larus argentatus - fuscus* group we have sequence DNA of over 1200 individuals (LIEBERS et al. 2001; LIEBERS & HELBIG 2002). No matter how desirable it would be to have voucher specimens of all these birds, few museums would be able and willing to prepare and store such a number of large-bodied specimens. Depending on the species involved, alternative kinds of voucher material can be archived, e.g. identifiable body parts (a set of feathers or dried wings in case of birds, skulls), alcohol-preserved whole specimens or photographs (labelled with sample identification number).

5. AVAILABILITY OF MATERIAL

The building up of tissue collections should not be limited by the research interests of their curators, but should ideally be targeted at the requirements of the scientific community as a whole. This means that taxonomical collections should be as broad as possible and material should be freely available to any researcher requesting it (perhaps against an appropriate fee, if necessary). In most cases, many aliquots can be obtained from a single sample so that repeated study of material from the same source is possible.

Museums should build up an information system enabling researchers to find out where they can obtain material of a particular species of interest. Several large museums already have publicly accessible inventories of their holdings that can be searched via the internet. It would be desirable to establish a universal information system among museums of a particular country or within Europe to enable a quick overview over collection holdings. But even before such a system is in place, simple lists on a museum's home page are an essential step in the right direction and do not require much work to be established and kept up to date.

By meeting the new demands of molecular systematic research, museums may counter the unfortunate trend of decreasing public awareness of the importance of their collections to modern science. In the long run, this may also foster an improved cooperation between „traditional" museum systematists working with morphological characters and molecular phylogeneticists.

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Methods of Systematic and Taxonomic Research on Passerine Birds: the Timely Example of the *Seicercus burkii* Complex (Sylviidae)[1]

Part 2 [2]

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Abstract. In 1999 *Seicercus burkii* auct. was recognized as a species swarm by two groups of investigators, and its components were analyzed. This paper summarizes what is known at present about this highly complex species group and includes some new findings of our own. The following species are distinguished: *S. burkii sensu stricto* (Himalayas), *S. whistleri* with the two subspecies *S. w. whistleri* (Himalayas) and *S. w. nemoralis* (foothills of the eastern Himalayas, N Burma), *S. valentini* with the two subspecies *S. v. valentini* (central and S China) and *S. v. latouchei* (SE China), *S. omeiensis* (China: Sichuan, Burma ?), *S. soror* (central and SE China) and *S. tephrocephalus* (central, S and SE China, NW Burma, N Vietnam). *S. affinis intermedius* (central and SE China) is included in the *S. burkii* complex on the basis of morphological and molecular-genetic characters; more information is needed regarding *S. a. affinis* (E Himalayas) and the *affinis* offshoot „*ocularis*" in Vietnam. Molecular-genetic investigations confirm a close relationship between the species with backs coloured a bright green, sharply outlined black crown-stripes and (with a single exception) consistent song-syntax characters. In the Chinese mountains up to four species, and in the Himalayas two or possibly three, can coexist on a mountain slope in well-defined vertical parapatry. Local sympatry can (except at the boundaries of the distributional belts) assemble up to three species in a high population density (China: Sichuan). The species of the *S. burkii* complex live at altitudes ranging from the subtropical foothills (in China down to about 550 m) to the cold-temperate zone of the subalpine coniferous forest belt (Nepal 3800 m: *S. whistleri*; China, Emei Shan 3099 m: *S. valentini*).

Key words. *Seicercus burkii* complex, species swarm, SE Asia, morphology, vocalizations, molecular genetics, speciation

1. INTRODUCTION

Large collections in zoological museums have long been an indispensable basis for taxonomic-systematic research. But it has become evident time and again that an equally essential element in new insights and incentives is meticulous fieldwork, which can reveal „fractures" in species previously regarded as homogeneous. Usually the first feature to be detected in the field is differences in the vocal repertoire. These indicate potential isolating mechanisms that can differentiate or separate allopatric or even sympatric populations. A relatively new development is that, owing to modern recording techniques, vocal documentation is now of such good quality that it ranks as high as morphological evidence. This calls for a re-evaluation of museum collections and a search for morphological characters that might complement the acoustical findings. Conversely, we know of examples in which material collected and compared using classical methods has given rise to discoveries subsequently confirmed in the field.

Even today, however, collections almost always lack not only song specimens, i.e. auditory documentation to accompany specific skins on deposit, but also the tissue samples that are now indispensable for studies in molecular genetics. The ideal combination is the individual bird as a scientific preparation, plus song recording and tissue sample. The consequence is that an initial suspicion that one is dealing with a cryptic species demands extensive fieldwork within the distribution area, all the more so if the situation turns out to be complex and the diversity of forms involved proves greater than expected. Small-scale distribution patterns, horizontal as well as vertical, vocalizations, playback experiments substantiated by recordings, and the availability of song specimens and tissue samples nowadays, in most cases, constitute an essential basis for further systematic, taxonomic and evolutionary analysis.

Our example *(Seicercus)* is a case typical of cryptic species, in that the decisive morphological characters only „take shape" when considered in the light of acoustic and molecular data, and hence demand especially careful data acquisition. Here we report on the *Seicercus burkii* complex (Sylviidae: standing close to, if not within *Phylloscopus*; see Martens et al.

1999: 283) of the Himalayas, China and countries bordering them to the south. Using many methods this group has been shown to be a species swarm. It has now become evident that *S. burkii* auct. is a complex of at least seven biospecies, each of which can be identified by several characters (although these are more or less inconspicuous). So far, however, their areas of distribution remain unclear, to say nothing of their ecological requirements. Nor are their behavioural characters known, apart from vocalization. Hence there is as yet no good explanation of the fact that in some mountainous regions as many as four species are present, in a strictly vertically segregated arrangement, whereas in others three species live side by side at the same altitude. In the present paper we summarize the current state of our knowledge about this recently unmasked species complex, so far unparalleled in the Palearctic and Indomalayan (Oriental) regions for sympatric species diversity and abundance.

2. MATERIAL

Our knowledge of the *burkii* complex is based on extensive field studies in Nepal (1969-2001, six trips during the breeding season, over two years of field sojourns, cf. Martens 1987, Martens & Eck 1995: 52-64) and China (1997-2002, four trips during the breeding season, 20 weeks of field sojourns in three provinces where *Seicercus* is present). During these studies a large amount of material was collected, including skins, song specimens and tissue samples. We concentrated particularly on the combined documentation of song and tissue samples to complement the skins, and for 22 individuals all these parameters are satisfied. One skin is accompanied only by a song recording. For molecular-genetic analysis 72 samples from seven species of the *burkii* complex are available. The external characters were studied by examining (about) 260 skins from various collections, 58 of which we collected ourselves. The sites where they were found, their vertical distribution, and the state of the gonads are thus unequivocally documented. Our specimens have been deposited in the Museum A. Koenig in Bonn (Nepal 1969-1995, 10 indiv.), the Museum für Tierkunde in Dresden (China, Nepal 2001, 47 indiv.) and the Zoological Museum, Chinese Academy of Sciences, Beijing (1 paratype of *S. omeiensis*).

3. GENERAL CONSIDERATIONS REGARDING THE *S. BURKII* COMPLEX

The *S. burkii* complex comprises medium-sized leaf warblers (ca. 7 g), all of which are remarkably uniform in colouration and patterning (Figs. 1, 2; colour plates and photos in Martens et al. 1999, 2000, Alström & Olsson 1999): bright to dull green back, bright yellow underside with fine differences in the shade of yellow, from lemon to nearly orange; head with two irregularly to sharply outlined black lateral crown-stripes and a green or grey median crown-stripe. A few grey to greenish feathers can be scattered through the basic colour of the median stripe. The eyes are surrounded by yellow feathers that form a delicate ring varying in width: widest in *S. affinis intermedius* (photos in Alström & Olsson 2000), narrowest in *S. omeiensis* (photo in Martens et al. 2000). Of the two Himalayan species *S. burkii* s. str. and *S. whistleri* (Figs. 1, 2), the latter has a distinctly broader and irregular eye ring broadened at the back edge and coloured a particularly luminous yellow (Figs. 1a, b). Only in *S. affinis* is there a gap at the top of the ring. Darker areas in the eye ring can be present (in all species?) at the upper edge of the eye, and occasionally there is a fine, sharp interruption at the back edge (*S. tephrocephalus*; *S. burkii* s. str., Plate 2a, page 25). In all species, the inner vanes of tail feathers T6 and T5 always bear white markings, which may also be present on T4; but never so in *S. soror* (only T6, though there is a hint on T5), and the same positions (T6-T4) are always occupied by large white areas in *S. w. whistleri* (Plate 1c, page 25) and *S. w. nemoralis*. There can be slight interindividual variability; for instance, in *S. burkii* s. str. (Plate 2c, d) and *S. tephrocephalus* the tip of T4 also occasionally has a white spot (quite large in Plate 2c, d).

4. DISTRIBUTION

The *S. burkii* complex, as it is currently understood, is distributed along the entire Himalayan chain, from an area to the west of northern Pakistan (Roberts 1992, *S. w. whistleri* according to high-altitude records during the breeding season) as far as SE Tibet (Alström & Olsson 2000; *S. burkii* s. str.), then from the forested regions on the eastern flank of the Tibetan plateau northwards to S Gansu (Lianhua Shan, S. v. valentini), and along the southern and northern flanks of Qin Ling (*S. v. valentini, S. omeiensis, S. soror, S. tephrocephalus*) to Guandong and to the Wuyi Shan in Fujian (*S. valentini latouchei, S. tephrocephalus?, S. affinis intermedius*). In the southwest the range is bounded by Mt. Victoria in Burma (*S. omeiensis, S. tephrocephalus, S. whistleri nemoralis*); although the position of its boundary towards the east is still unknown, it extends to northern Vietnam (Fan Si Pan, *S. tephrocephalus*; Alström & Olsson 1999) and occasional observations have been made in southern Vietnam (*S. affinis „ocularis"*, Robinson & Kloss 1919). It is likely that species of the *burkii* complex are present throughout central and southern China in (still) forested mountains above ca. 500-600 m, perhaps in dense populations, even in secondary growth. Lowland plains are evidently avoided (cf. Cheng 1987, 2000).

S. poliogenys (NE India) is probably closely related to the *burkii* complex, but *S. xanthoschistos* is not, nor are the southeast Asian species with brown head coloration: *S. castaniceps, S. montis* and *S. grammiceps*.

5. PLUMAGE PROPORTIONS OF THE *SEICERCUS* SPECIES

It has long been recognized that deviations in relative dimensions, such as the lengths of wings and tail, are among the more significant diagnostics. During our preliminary comparisons, some individuals of the Himalayan „*Seicercus burkii*" were found to have conspicuously short tails, and this did indeed prove an important indicator. Consider these relative tail lengths: in 13 *S. burkii* s. str.: 76-80 %, x=78.3 s.d. 1.52; in 73 *S. w. whistleri* 79-88 %, x =83.4 s.d. 2.00; *S. w. nemoralis s.str.* is again relatively long-tailed (see below under *S. whistleri* and MARTENS et al. 1999: 287, Fig. 4). Among the species sympatric in China the new species *S. soror* is distinctly short-tailed: relative tail length 74-81 %, x=77.3 s.d. 1.71 in comparison to *S. omeiensis* ([77.4 %] 82-86 %, x=83.9, s.d. 1.26 n=10). Corresponding to this relatively short-tailed condition is a somewhat elongated wing with a tendency towards a higher hand-wing index (x=16.1 %, s.d. 0.87 in 11 *omeiensis* as opposed to x=18.5 %, s.d. 1.61 in 24 *soror*). The hand-wing index, firmly established as a character for many decades, was confused with the primary projection by ALSTRÖM & OLSSON (2000: 499) (for details on this subject see ECK & ENGLER 2001: 362-363). *S. tephrocephalus* („*distinctus*"), n=52 from its entire range, has a wing length of at most 57 mm, smaller than *S. omeiensis*, but the same relative tail length as the latter, x=84.3 %, s.d. 2.11, and a distinctly lower hand-wing index, n=52 *tephrocephalus* x=13.9 %, s.d. 2.00; n=11 *omeiensis* x=16.1, s.d. 0.87. The largest species is *S. valentini*, with measurements for the ssp. *valentini* as follows: wing length maximally 65 mm; hand-wing index x =16.7 %, s.d. 1.22; relative tail length x=82.7 %, s.d. 2.11.

6. TAXONOMY

Despite certain differences the analyses of the „*burkii* diversity" by the Swedish group (ALSTRÖM & OLSON 1999) and the German group (MARTENS et al.1999) are extremely similar. MARTENS et al. (1999) were more reluctant to combine vicariant taxa into polytypic species. They named a total of eight taxa, the combination of which to form biospecies was not clearly discernible in all cases. ALSTRÖM & OLSSON (1999) defined five species, two of which were each divided into two subspecies. This should be accepted. One difference between the two interpretations lies in the geographical extent of the two subspecies of *S. whistleri*, and of the southern range limit of *S. omeiensis*. A discussion of these points follows below.

S. tephrocephalus (ANDERSON, 1871): ALSTRÖM & OLSSON (1999) assigned to this taxon three population groups („group 4", „group 5", „group 6") that they regarded as conspecific. However, in the present interpretation the name comprises two species, *S. tephrocephalus* and *S. omeiensis*.

6.1. *Seicercus tephrocephalus* (ANDERSON, 1871)
[= *tephrocephalus* „group 4" (and „group 5") in ALSTRÖM & OLSSON 1999].

ALSTRÖM & OLSSON (1999) established a neotype for *Culicipeta tephrocephala* ANDERSON, 1871, because the type material in the Calcutta Museum has evidently been lost. This neotype (New York 450451) can be identified as *Cryptolopha burkii distincta* LA TOUCHE, 1922. The small size (wings 51.0 mm, tail 40.5 mm), the sharply outlined black lateral crown-stripes and the grey colouration between crown-stripes and eye argue for this interpretation. ALSTRÖM & OLSSON (1999) also describe these populations („group 4", „group 5") as distinctly short-winged (maximum 57 mm). MARTENS et al. (1999) referred to this readily identifiable form as *S. distinctus* (LA TOUCHE). The illustration of the tephrocephalus type in an excellent colour drawing by KEULEMANS in ANDERSON (1878, Plate L) is in marked contrast to the description of the neotype of *S. tephrocephalus* by ALSTRÖM & OLSSON (1999) (cf. Plate 1 in Ibis 141, 1999). *S. tephrocephalus* (sensu ANDERSON 1871, 1878) and *S. distinctus* (sensu MARTENS et al. 1999) are very different species within the *burkii* complex, in their size, colouration, and patterning. It is our opinion that ANDERSON (1871, 1878) and ALSTRÖM & OLSSON (1999) were referring to different taxa in the *burkii* complex, and that the neotype does not conform to ANDERSON'S intentions. According to this neotype declaration, *distinctus* (LA TOUCHE) sensu MARTENS et al. 1999 is the same taxon as *tephrocephalus* „group 4" sensu ALSTRÖM & OLSSON. Species *S. distinctus* of MARTENS et al. (1999) must therefore now be called *S. tephrocephalus*. This leaves the taxon originally established by ANDERSON without a name, so the lost name must be replaced by *S. omeiensis* MARTENS, ECK, PÄCKERT & SUN, 1999. A tissue sample of a winter visitor belonging to the *burkii* complex collected in Cambodia (F. STEINHEIMER leg., Tring 2000.5.42), and exhibiting the characters of *tephrocephalus* sensu ANDERSON (1871, 1878), was found to have an *omeiensis* haplotype (cyt b). Hence the northern (*omeiensis*; W China) and southern populations (*tephrocephalus* sensu ANDERSON, non sensu ALSTRÖM & OLSSON; Burma), which differ only slightly in colour, should be united in a single species. All other names in the *burkii* group are unavailable for the southern population („*tephrocephalus*"), as they have been assigned to other valid

species or subspecies. To minimize the potential for confusion, in the present paper we use the nomenclature that results from the situation just described. For the moment, it provides the greatest stability.

Distribution: widely distributed in the tropical/subtropical part of southeastern Asia (in China as far north as Shaanxi: Taibai Shan, also Burma, N Vietnam).

6.2. *Seicercus omeiensis* Martens, Eck, Päckert & Sun, 1999 (= *tephrocephalus* „group 6" sensu Alström & Olsson, 1999), *S. omeiensis* in Alström & Olsson (2000).

S. tephrocephalus (syn. *distinctus*) inhabits China, along with *S. omeiensis* (= *tephrocephalus* „group 6" sensu Alström & Olsson), as a species sharply separated in every respect. The taxon *tephrocephalus* (Anderson, 1871) was considered by Martens et al. (1999), on the basis of the colour illustration by Keulemans (see also Hartert 1907: 496) and a number of skins from Burma, not to be identical to either *distinctus* La Touche or differently coloured Chinese representatives (= *S. omeiensis*). The Burmese birds (12 specimens from Burma: Mt. Victoria, Mt. Popa, Dudaw Taung, Maymyo), for which neither vocal nor genetic characters were known, have distinctly yellower upperparts than the Chinese *omeiensis*, but it is necessary to compare series to notice the difference. In 1999, it seemed appropriate to keep all three forms taxonomically separate, and to wait until more information is known about them before linking them. This proved to be correct. It still needs to be determined whether *omeiensis* s.l. breeds in Burma; two individuals were found in Karenni/Burma on 15. and 16.IV.1939 (Tring: 1948.80.883 and .884), which is at least the beginning of the breeding season.

Distribution: a species with (as far as is known) a small range; specimens found at four sites in Sichuan (Emei Shan, Wawu Shan, Qincheng Back Mts.) and Shaanxi (Taibai Shan); Burma?

6.3. *Seicercus burkii* s. str. (Burton, 1836) – Plate 2

Both groups of authors agree in giving this name to the populations at lower altitudes in the Himalayas to distinguish them from higher-altitude populations. This is a species with bright green dorsal plumage, predominantly green median crown-stripe and lateral crown-stripes strikingly set off in black (Plate 2a-c). Over the whole area *S. burkii* is a vertical vicariant of *S. whistleri*, always occupying the lower distributional belt.

Distribution: Himalayan chain, westernmost documentation in Garhwal (Irani, 30.VI.1914 and Dsoli/Tarag-Tal, 23.V.1925; specimens Tring 1949whil .12799 and .12800); in the SE the range extends into

the Garo Hills/Assam (Ann Arbor 188750, 11.IV.1950) and to SE Tibet (Alström & Olsson 2000). **Locus typicus**: originally not specified, by neotype establishment „Sikkim" (Alström & Olsson 1999).

6.4. *Seicercus whistleri* Ticehurst, 1925 (Alström & Olsson 1999, 2000: polytypic species with two ssp: *S. w. whistleri* and *S. w. nemoralis*). – Plate 1.

According to Alström & Olsson (1999, 2000), *S. whistleri* is polytypic. In addition to the nominate form in the western and central Himalayas, the ssp. *nemoralis* Koelz, 1954 is said to inhabit the E Himalayas from Nepal, NE India (Lushai Hills) and Burma as far south as Mt. Victoria. Topotypical *nemoralis* (Lushai and Naga Hills, NE India), as well as specimens from Burma, have relatively longer tails than the central Himalayan whistleri (including topotypical birds), which in turn are a uniform group. The breast of *nemoralis* is delicately orange-coloured („brownish" in Alström & Olsson 1999, 2000), but because this feature is not constant between *nemoralis* and *whistleri* (Nepal, Sikkim, Bhutan; cf. Alström & Olsson 1999, 2000), colour characters are not suitable for subspecies separation. Therefore Martens et al. (1999) and Martens & Eck (2000) initially employed the relative tail length (l. c. 1999: Fig. 4) for identification. They found in *whistleri* (for distribution see below) 79-88 %, x=83.4 s.d. 2,00 (n=73), of which in 28 from Nepal, including E Nepal x=83.4 % s.d. 1.98, and in *nemoralis* (for distribution see below) 83-92 %, x=86.9 s.d. 2.61.

The conspecificity of *whistleri* and *nemoralis*, which we are treating separately for the time being, remains to be corroborated. No vocalization recordings or cyt b sequences of *nemoralis* from the type locality or from Burma have been published, or are otherwise available to us. Acoustically, and in their molecular genetics, all the investigated Nepalese populations of *S. whistleri* are uniform, apart from a total of seven slightly differing haplotypes (13 samples, from NW Nepal to the catchment region of the Arun in E Nepal, 700 km NW-SE extent).

Distribution: that of the two subspecies is unclear, depending on the criteria employed, but there is likely to be no sharp boundary. Nevertheless it is reasonable to consider *nemoralis* as limited to the easternmost Himalayas and foothills and to N Burma. Subdivision according to plumage proportions (see above): *S. w. whistleri* from the Pakistan NW Himalayas along the Himalayan chain into the eastern Indian Himalayas (Garo and Khasi Hills) and as far as SE Tibet; *S. w. nemoralis*: southern foothills of the eastern Himalayas (Lushai Hills and Naga Hills), presumably the mountains in adjacent Burma, south to Mt. Victoria.

6.5. *Seicercus valentiui* (Hartert, 1907) (Alström & Olsson 1999, 2000: polytypic species with two ssp: *S. v. valentini* and *S. v. latouchei*)

This is the largest species, with wing length up to 65 mm, followed by *S. whistleri*, the wing length of which reaches 62 mm. Both species inhabit the highest mountain slopes of all *burkii* complex members.

Sonagrams of the southeastern ssp. *latouchei* (Prov. Fujian) (Alström & Olsson 1999: Fig. 9h) confirm that this population does belong to *S. valentini*, though it is widely disjunct from the rest of the range in central China (Prov. Sichuan, Shaanxi, Gansu). The subspecific separation is based on fine colour differences (and perhaps smaller dimensions of *latonchei*).

Distribution: we have own material for the nominate form from Gansu (Lianhua Shan), Shaanxi (Taibai Shan), Sichuan (Omei Shan, Wawu Shan); autumn birds from Yunnan. **Locus typicus**: Taibai Shan (Hartert 1907). – *S. v. latouchei*: SE China, Prov. Fujian and Hubei.

6.6. *Seicercus soror* Alström & Olsson, 1999

Martens et al. (1999) had no material for *latouchei* Bangs, and hence used the name provisionally and, as it turned out, erroneously for a new species inhabiting medium-altitude sites in the mountains of Sichuan and Shaanxi; at that time no type material was accessible. This taxon was described by Alström & Olsson (1999) as a new species, *S. soror*.

Distribution: Shaanxi, Sichuan, Guizhou, Fujian; in winter as far as Indochina, south to Cambodia (Eames et al. 2002).

6.7. *Seicercus affinis* (Hodgson, 1854) (Alström & Olsson 1999: not included, but see Alström & Olsson 2000)

According to our present understanding two disjunct (?) areas exist: *S. a. affinis* (Hodgson, 1854) in the eastern Himalayas from West Bengal through Bhutan and Arunachal Pradesh to NE India, Burma, N Vietnam (Watson 1986); and *S. a. intermedius* (La Touche, 1898) in SE China in the provinces of Fujian and SW Yunnan (Cheng 1987). The latter has recently also been found widely disjunct in Sichuan (Emei Shan; Martens et al. 1999; Martens & Eck 2000: *Seicercus* spec.; Alström & Olsson 2000). The Ta-wie Mts./SE Yunnan are inhabited by *S. a. affinis* according to Watson (1986: 259), but by *S. a. intermedius* according to Cheng (1987: 824)!

Molecular-genetic data place the eastern *S. a. intermedius* (Emei population) within the *burkii* complex.

In view of its conspicuously broad eye-ring with a gap at the top, *intermedius* was originally classified as a separate species (La Touche 1898), but later was incorporated into the Himalayan form. The Fujian population is notable in that the median crown-stripe can be a pure green or a pure grey (see Jordans & Niethammer 1940: 125-126; Stresemann 1940). The two specimens from Emei Shan have a grey median crown-stripe. The eye-ring is wider in the Fujian population than in that of the Emei (our own material, Museums Bonn and Beijing; Alström & Olsson 2000, Fig. 2), but it is yellow in both. The relationships of *S. a. intermedius* to the western nominate form and the Vietnam population regarding morphology (shape and colour of the eye-ring, dimensions, proportions), vocalizations, and molecular genetics, have not been clarified.

7. SURVEY OF THE SPECIES AND SUBSPECIES

7.1. Group 1

Seicercus affinis

Seicercus affinis affinis (Hodgson, 1854)
    Loc. typ.: Nepal
    Syn. ?*Cryptolopha tephrocephala ocularis* Robinson & Kloss, 1919
    Loc. typ.: Lang Bian, S. Annam
Seicercus affinis intermedius (La Touche, 1898)
    Loc. typ.: Fukien
    Syn. *Cryptolopha burkii cognita* La Touche, 1922
    Loc. typ.: Kuatun, NW.Fukien [Fujian Prov.]

Seicercus burkii

Seicercus burkii (Burton, 1836)
    Loc. typ. restr.: Sikkim

Seicercus tephrocephalus

Seicercus tephrocephalus (Anderson, 1871)
    Loc. typ.: Bhamô/Burma
    sensu Alström & Olsson 1999: *tephrocephalus* „group 4"
    Syn. *Cryptolopha birmanica* Berezowski & Bianchi, 1891
    Loc. typ. restr.: Lower Pegu/Burma, according to tests by Alström & Olsson 1999: 555
    Syn. *Cryptolopha burkii distincta* La Touche, 1922 (= *S. distinctus* sensu Martens et al., 1999)
    Loc. typ.: Mengtz/SO-Yunnan

7.2. Group 2

Seicercus whistleri

Seicercus whistleri whistleri Ticehurst, 1925
Loc. typ.: Dharmsala, Punjab

Seicercus whistleri nemoralis Koelz, 1954
Loc. typ.: Sangau, Lushai Hills

Seicercus valentini

Seicercus valentini valentini (Hartert, 1907)
Loc. typ.: Tsinling Mountains (in forest belt)
[Qing Ling, Shaanxi Prov.]

Seicercus valentini latouchei Bangs, 1929
Loc. typ.: Kuatun, Fukien [Guadun, Fujian Prov.]

Seicercus omeiensis

Seicercus omeiensis Martens, Eck, Päckert & Sun,
1999
Loc. typ.: Mt. Emei, 2330 m, Sichuan Prov.
= sensu Alström & Olsson 1999: *tephrocephalus*
„group 6“
ssp. in Burma ? (= *tephrocephalus* sensu Martens
et al. 1999)

Seicercus soror

Seicercus soror Alström & Olsson, 1999
Loc. typ.: Hopiachen, Sichuan Prov.
= sensu Martens et al., 1999: S. „latouchei“, nec
latouchei Bangs, 1929

8. SPECIES COMMUNITIES, BOTH HORIZONTAL AND VERTICAL

Previous experience has taught us that the species of the *burkii* complex are arranged in a vertical sequence in the individual mountain massifs, encountering one another at contact zones that are often sharply defined. Only in such a zone do two „altitudinal vicariants“ live effectively side by side in a confined space, so that a field observer, with luck, can hear both of them at the same time at a single site. Such cases have been described for Nepal and China (Sichuan: Emei Shan, Martens et al. 1999; Alström & Olsson 2000). The situation in the Taibai Shan (Shaanxi) is evidently the same, although documented in less detail by our own data sets (Martens et al. 1999). According to heterogeneous historical skin material, this stepwise vertical distribution is also indicated for other Chinese mountains (Alström & Olsson 1999, Fig. 12), as well as for Mt. Victoria in Burma (Myanmar) (Martens et al. 1999; Alström & Olsson 1999). However, when data from various mountains are combined (Alström & Olsson 1999, Fig. 12; cf. the individual data for S. *burkii* s. str. and S. *whistleri* in Nepal in Martens &

Eck 1995; Martens et al. 1999), it is readily apparent that the vertically adjacent range belts can overlap to varying degrees. With five species of the *burkii* complex, this „layering“ of species looks different in various parts of the Chinese mountains. Nevertheless, the sequence of species is always maintained, from (sub)tropical ones to those with a cool-temperate affinity. In the case of China, the species sequence from the base of the mountains into the peak regions appears as follows: S. *tephrocephalus* („distinctus“), S. *soror*, S. *affinis intermedius*, S. *omeiensis*, S. *valentini*. If there is not enough vertical space for both of them, either S. *tephrocephalus* or S. *soror* lives at low altitude, closer to the peak comes S. *omeiensis*, and above that the S. *valentini* belt regularly forms the upper edge of the range. These observations indicate distinct ecological/ethological incompatibility at a given site, at least in the contact zones. However, it is unclear to what extent potentially broader belts are reciprocally limited by competition at the contact zones. Would the individual belts be wider if a mountain massif were inhabited by fewer species (than three or even four), or just one? Earlier individual data indicate that ecological exclusion between the species is not complete, but it remained open whether it was a matter of only isolated „errors“ (occasional *burkii* in the *whistleri* area of Nepal, *soror* in the *valentini* area of the Emei, or *affinis intermedius* regularly in the *soror* area of the Emei) or whether local syntopy is frequent or even routine. In the Back Mts./ Qincheng Shan (70 km NW of Chengdu, Sichuan, 30°53' N 103°28' E) during the period 11.-16.V.2000, J. Martens and H.-Y. Sun found three species living together at high density at 1200 m, and documented this finding by skins, tissue samples and tape recordings: S. *soror* (3/4/6: skins/tissue samples/recordings), S. *tephrocephalus* („distinctus“) (2/4/1) and S. *omeiensis* (3/3/5). Almost all the documentation was obtained by chance (only 2 intentionally collected song specimens) at three mist-net sites in secondary deciduous forest. The vertical and horizontal extents of this coexistence belt could not be determined. Here a higher degree of ecological compatibility is indicated, and simultaneously a striking niche formation.

9. BIOACOUSTICS

The high degree of morphological similarity between the species in the *burkii* complex ought to have produced conspicuous variation in their vocalizations, but some species are very similar even in this respect. However, for most of the species clearly distinctive characters can be detected, especially in the case of the calls. These selective features are all the more important in view of the fact that in regions of sympatry, at
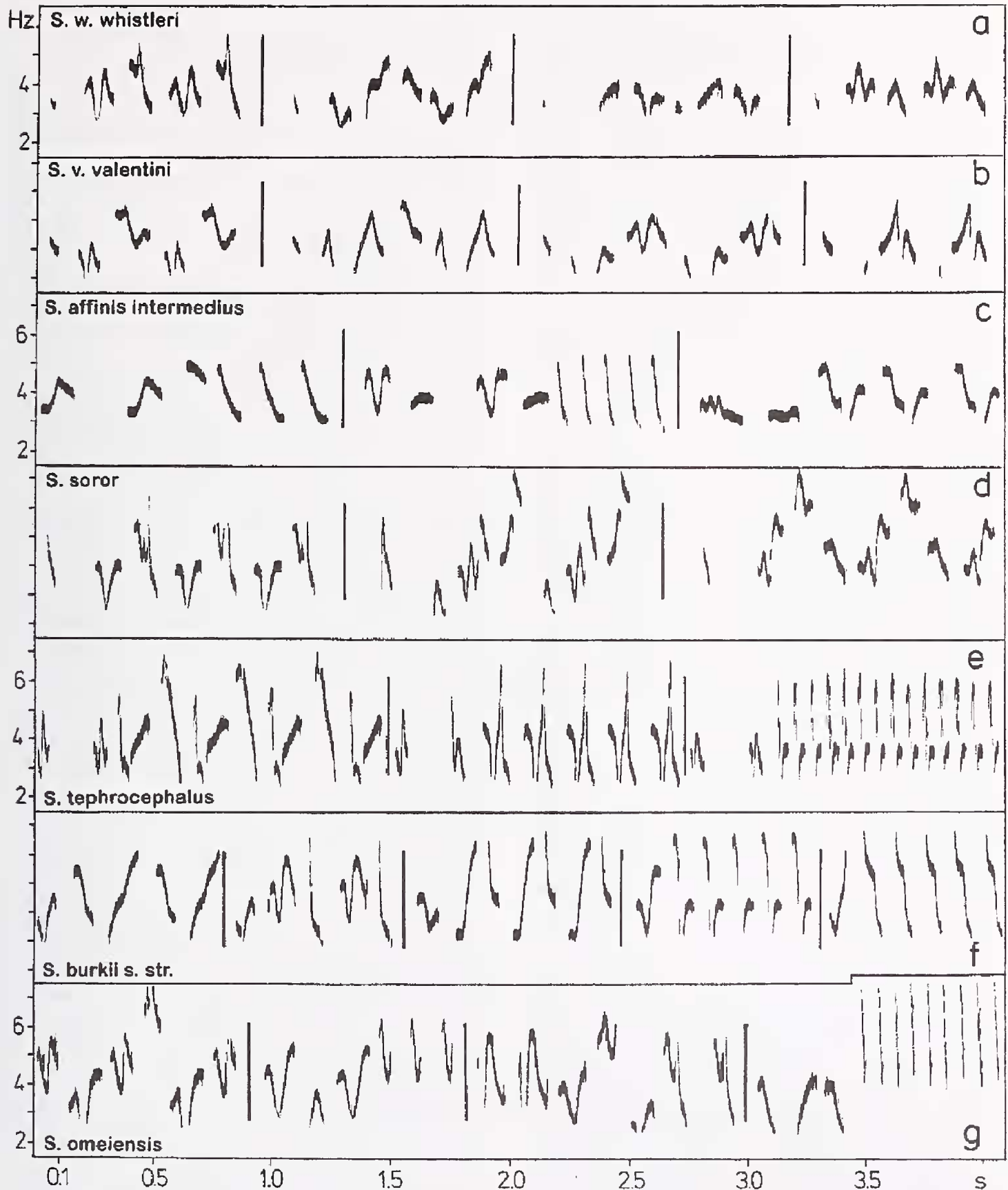
Fig. 1: Three, four or five verses of territorial song, respectively, of one male each of seven *Seicercus* species, **a**: *S. w. whistleri*, Irkuwa Khola, Bhojpur Distr., Nepal, 2750 m, 7 April 2001; **b**: *S. v. valentini*, Wawu Shan, Sichuan, China, 2750 m, 30 May 2000; **c**: *S. affinis intermedius*, Emei Shan, Sichuan, China, 1200 m, 21 May 2000; **d**: *S. soror*, Foping, Shaanxi, China, 900 m, 9 May 2000; **e**: *S. tephrocephalus*, Houzhenzi, Shaanxi, Taibai Shan, China, 1300 m, 8 May 2000; **f**: *S. burkii* s. str., Irkuwa Khola, Bhojpur Distr., Nepal, 2160 m, 15 April 2001, **g**: *S. omeiensis*, Wawu Shan, Sichuan, China, 1800 m, 29 May 2000. – All recordings J. MARTENS.

least at the parapatry junctions of the vertically arranged range belts, certain species live within hearing distance of one another. Vocalizations would be expected to be especially significant here as premating

isolating mechanisms to prevent interspecific mating. In characteristics of the strophe organization (syntax structures), and in the measurements we have so far made to characterize the songs, some remarkable similarities have been found between individual species: the songs of *S. burkii* (Nepal) and *S. omeiensis* (China: Sichuan) resemble one another so closely that they can hardly be distinguished in population and repertoire comparisons for individual males (Fig. 1f, g). In two playback experiments, however, *S. omeiensis* failed to „understand" the song of *S. burkii* (Emei Shan, VI 1998). In contrast, local conspecific song of *S. omeiensis* always elicited a vigorous territorial response.

The songs of the seven species of the *burkii* complex that have so far been examined have a simple syntactic structure. However, the individual repertoire is not clearly discernable, because each male employs many conspicuously different strophe types. Each of these is produced with high precision and no variability. A male of any of the species that sings continuously for some time will go through its entire repertoire, often comprising more than 20 different strophes, and then start over again or subdivide the repertoire (irregularly) into small blocks of strophes, which in turn are repeated with no fixed rules.

Two species groups can be clearly separated on the basis of strophe structure: *S. whistleri, S. valentini* and *S. soror* on the one hand (Fig. 1a, b, d) and *S. burkii* s. str., *S. omeiensis, S. tephrocephalus* („distinctus") and *S. affinis intermedius* on the other (Fig. 1f, g, e, c). In the strophes of the first group, a temporally offset introductory element with descending frequency is followed by an element group (called „phrase" by Alström & Olsson 1999) composed of two (rarely three) elements. This element group is repeated once or rarely twice, which completes the strophe. Within this group, *S. whistleri* and *S. valentini* (which are allopatric at high altitudes in the Himalayas and Chinese mountains) are especially similar in their songs, which is (also) striking with respect to the small frequency bandwidth of the strophes (x=2.4 kHz in both species, n=15 for each). Slight differences are present in the *whistleri* and *valentini* songs. For instance, the *whistleri* song is 0.4 kHz higher than that of *valentini*, in both the lower and upper frequency range. *S. soror* (Fig. 1d) stands out from both of these in having a much broader frequency band (x=4.4 kHz; n=20).

The strophe syntax is more irregular in the second species group. A common feature is that each male sings many strophes that end in a trill, the components

of which are sometimes close together and sometimes further apart (Fig. 1f, g, e, c, „tremolo" and „trill" in Alström & Olsson 1999). This applies to 80 % of the trophes of *S. affinis intermedius*, 51 % for *S. tephrocephalus*, 48 % for *S. omeiensis* and 39 % for *S. burkii* s. str. The songs of *S. omeiensis, S. tephrocephalus* and *S. burkii* have a broad bandwidth (x=4.0-4.6 kHz), whereas those of *S. affinis intermedius* are very narrow (x=2.3 kHz). In both sonagram and auditory impression the songs of *S. omeiensis* and *S. tephrocephalus* closely resemble one another. That of *S. tephrocephalus* always begins with one or two broad-band introductory elements, which are either identical or very similar to the typical double call (Fig. 1e). The song of a *S. tephrocephalus* in a Vietnamese population was illustrated by Alström & Olsson (1999). From the available data, no geographical variability with respect to the Chinese populations (Shaanxi, Sichuan) can yet be discerned.

All seven species use quite different and clearly distinguishable calls (cf. Martens et al. 1999; Alström & Olsson 1999). These may be brief, steeply rising *(S. burkii* s. str.*)* or softer, descending *(S. valentini)* individual calls, or groups of two sharp calls each descending in frequency *(S. tephrocephalus, S. omeiensis, S. whistleri)*. Complicated „call songs" are produced by *S. soror* and *S. affinis intermedius*, and in the latter species each individual has a call repertoire. In characterizing the calls, Alström & Olsson (2000) emphasize that apart from one case their results agree well with those of Martens et al. (1999); only for *S. omeiensis* did their conclusions differ. The songs recorded by Alström & Olsson (1999, 2000) were evidently not exactly in the focus of the microphone during the recording process. When centring is imprecise, the fine click-like call and its closely apposed overtone fuse in the sonagram. In the present case the result is a structure very similar to the double calls of *S. tephrocephalus* (Alström & Olsson 1999, Fig. 11b from recording at Emei Shan). *S. tephrocephalus* has not been documented in this locality.

10. MOLECULAR GENETICS

In our study of the cytochrome-b gene (Päckert et al., in prep.) seven taxa of the *burkii* complex were included: *S. burkii* s. str. (2 specimens, 1 locality E Nepal), *S. w. whistleri* (12 spec., 7 loc. W and E Nepal), *S. v. valentini* (15 spec., 4 loc. China: Sichuan, Gansu, Shaanxi), *S. omeiensis* (12 spec., 5 loc. China; Sichuan, Shaanxi; Cambodia), *S. soror* (15 spec., 4 loc. China: Sichuan, Shaanxi; Cambodia), *S. tephrocephalus* („distinctus") (12 spec., 3 loc. China: Sichuan, Shaanxi; N Thailand) and *S. affinis intermedius* (2 spec., 1 loc. China: Sichuan). All but three originate from the respective breeding areas.